

On the Life History of *Nereis grubei* (Kinberg), a Polychaete Annelid from California¹

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RELATIVELY LITTLE INFORMATION is yet available on the life histories of nereid polychaetes from the eastern Pacific. Johnson (1943) has raised some intriguing problems concerning *Nereis vexillosa*, which have not been further explored, and Smith (1950) has reported details of the life history of *Nereis limnicola* (= *Neanthes lighti*), an interesting viviparous, euryhaline species. Information is also available for a southern Californian population of *Nereis grubei*, a species which reproduces more typically. The present paper deals with a central Californian population of *N. grubei* from Pescadero Point, Monterey County. Interesting differences between these two populations with respect to physiology and breeding season have come to light during the course of an investigation of nereid metamorphosis (Schroeder, 1967).

HABITAT

At Pescadero Point, Monterey County, California, *Nereis grubei* occurs on an exposed coast where the surf can be quite violent, even though offshore kelp beds are well developed. The intertidal region is composed chiefly of large boulders covered with abundant algae of many species. The worms may be found here in two different situations, in which their abundance varies with the season. During the spring and summer they are most readily found in the sandy substrate beneath the common red alga *Gastroclonium coulteri*. Some specimens may be found in this situation throughout the year, but from the beginning of October until the middle

of February the animals are more abundant in holdfasts of the highest specimens of the brown kelp *Egregia menziesii*. In order to collect the animals from their burrows in the kelp the holdfasts must be removed from the rock with a hammer and chisel and carefully dismembered. During the summer only a few, usually very small specimens can be recovered from these holdfasts; this was tested by allowing summer-collected holdfasts to stagnate in a pan until animals emerged from the inaccessible interstices. It seems probable that the worms move into the kelp holdfasts for the winter, when the surf is most violent. Such seasonal habitat shifts are known in other intertidal animals from this area as well (e.g., the isopod *Idothea montereyensis* [see Lee, 1966]).

The habitat reported by Reish (1954b) for the species at Point Fermin in southern California appears to be somewhat different. He found *N. grubei* in algal tufts in or between tidepools scoured from a wide, flat rock ledge. The ledge is strewn with scattered boulders and sheltered from the surf by offshore kelp beds. At Point Fermin the worm was found to be associated with a number of different species of algae, chief among which is *Cladophora trichotoma*. This alga occurs in central California as well, and a search through tufts of it near the Hopkins Marine Station, not far from Pescadero Point, failed to yield any specimens of *N. grubei*, although the worm occurs beneath *Gastroclonium* in the same area. Although Reish surveyed the algal associates of the species at Point Fermin he mentions neither *Egregia menziesii* nor *Gastroclonium coulteri*, the two major algal associates at Pescadero Point. The former is not found south of Point Conception, but the latter is recorded from as far south as San Diego (Smith, 1944). It thus appears that the more northerly population favors *Gastroclonium*, despite the presence of *Cladophora*, and that the opposite is true for the southern population

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(although I do not know whether *Gastroclonium* is abundant at Point Fermin).

In an ecological study at the Hopkins Marine Station, not far from Pescadero Point, small numbers of *N. grubei* were found by Glynn (1965) in association with another alga, *Endocladia muricata*. This alga is not included in the list given by Reish for the southern California population.

OOGENESIS AND METAMORPHOSIS

Nereis grubei was collected every two weeks at Pescadero Point, Monterey, California, for a period of 17 months. During the period of oogenesis the average oocyte diameter was determined for a number of specimens from each collection; the number of specimens so determined varied with experimental requirements. All diameters were measured from fresh coelomic samples with a calibrated ocular micrometer and a compound microscope. Fixation in Bouin's fluid made up with picric-acid-saturated sea water was found to cause an irregular expansion of the oocytes (Schroeder, 1966). In some animals, oocytes of considerably different diameters were present, but in most of these the recorded diameters fell into distinct size classes. In such cases only the average diameter of the largest size class was utilized in the life history study. In the few cases in which size classes were not evident, the diameters of all the oocytes from a single animal were averaged together. It is probable that such figures are lower than the value truly comparable to the others. The average oocyte diameter was used as an index to the age of female animals.

Oocytes could be found in at least a few animals throughout the year. Oogonia and tiny oocytes appear in June, when very few maturing females remain from the previous year's spawning group. The oocytes probably reach maturity (about 200μ) in 7–8 months. The young oocytes grow slowly through the fall and early winter, and the population gives rise to several swarms between mid-February and mid-June. The occasions on which nearly mature females were found in the field are indicated by the short vertical bars at the top of Figure 1. (The O in mid-March represents a day on which metamorphosing animals were expected

and sought, but not found.) Such nearly mature animals probably swarmed within a couple of days of being observed, although swarming itself was never observed.

The fact that maturing animals are found on separate occasions, and not in intervening periods, implies that specimens within the population mature at different times. It should thus be possible, in midwinter population samples, to separate animals destined for different spring-time spawnings.

Oocytes have been shown to grow at two different rates, both in *N. grubei* (Schroeder, 1966) and in *N. diversicolor* (Clark and Ruston, 1963). Thus in *N. grubei* the oocyte growth rate (rate of diameter increase) seems to accelerate when the oocytes are about 100μ in diameter, and it is at about this time that the first histological signs of metamorphosis can be detected (Schroeder, 1967). This fact is utilized in Figure 1 in an attempt to follow the development of each monthly swarm within the population as a whole. The dotted lines are projections based upon the apparent time of swarming, estimates of the growth rate during the two phases, and the recorded oocyte diameters. It is assumed that the oocyte growth rates are similar in the component animals of successive spawnings. Each month on the graph has been subdivided into 3-day periods, so that the positions of the points within a month are significant to within three days. It will be seen that during the fall animals with oocytes of a wide range of sizes are present, but that these are not separable into distinct groups until December, when most specimens can be assigned to a spawning group, even though the oocytes are still small and growing slowly. It is possible that the different spawning groups are distinct from the initial moment of oogonial differentiation, but the variability of oocyte sizes present in young animals prevents their recognition.

A number of animals was maintained in the laboratory over a period of weeks and the growth of their oocytes was checked by repeated sampling. These sampling points have also been included in Figure 1 and are connected with heavy lines. It will be seen that all but two of these animals were derived from the April spawning group, while two others metamorphosed sooner and were closer to the March

OOCYTE DEVELOPMENT AND METAMORPHOSIS IN *NEREIS GRUBEI* AT PESCADERO POINT, MONTEREY CO. CALIFORNIA

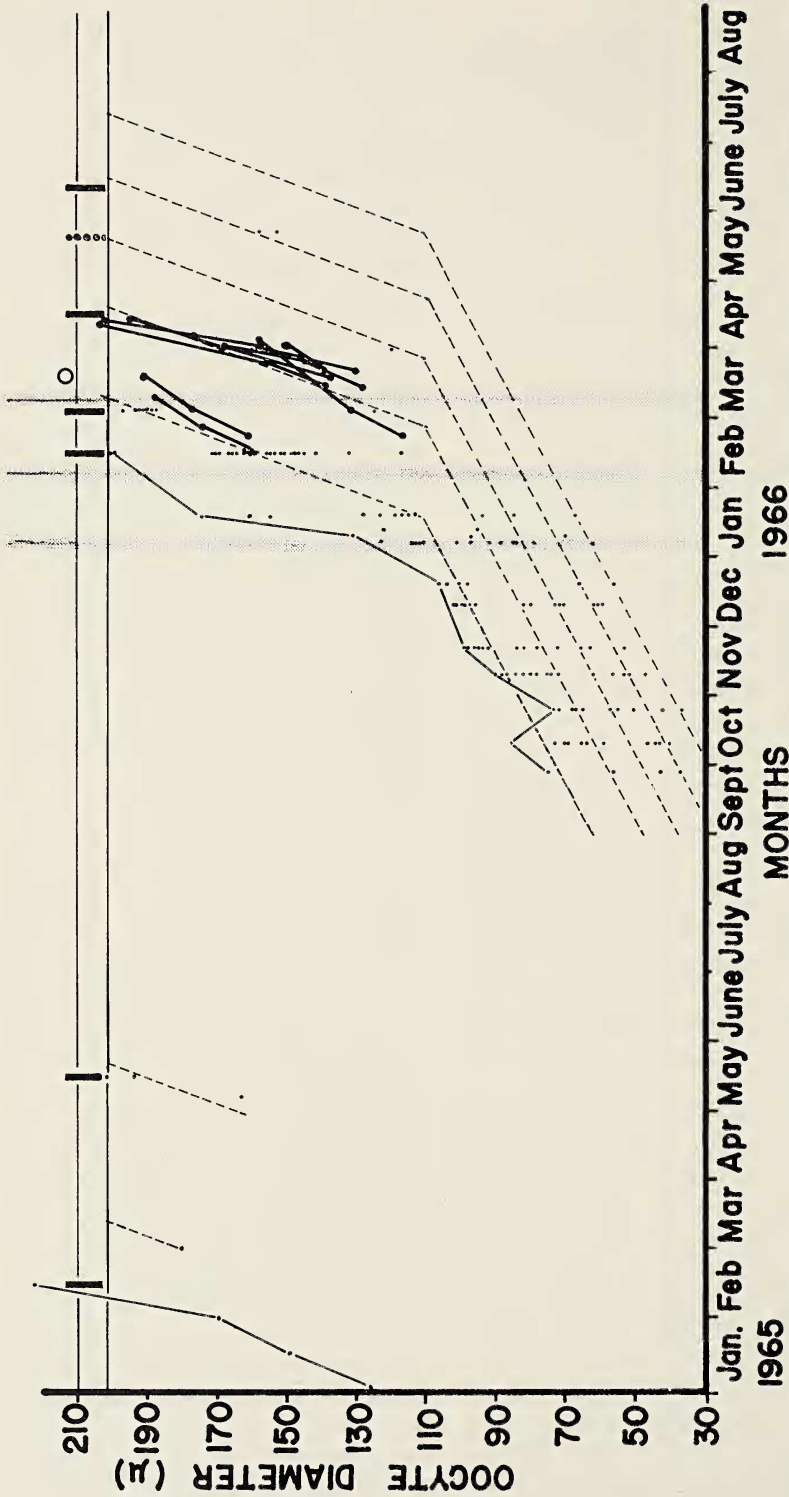


FIG. 1. Oocyte development and swarming in *Nereis grubei* at Pescadero Point, Monterey County, California. Each point in the 1966 series represents the average oocyte diameter of an animal collected on the date indicated. Dotted lines represent the postulated progress of several subgroups within the population toward their respective swarming dates. Solid lines represent growth rates from individual animals. The solid line on the left connects the largest oocyte diameters found in each collection. Days on which very mature specimens were found in the field are indicated by a vertical line through the delimited zone which includes the range of oocyte diameters found in swarming females. The zero represents a day on which no such animals were found; the dotted line in this group (in May) is an estimated swarming date based on laboratory observations. Vertical stippled lines indicate the time of the full moon through the collecting period. The 1965 collections were incomplete due to inadequate knowledge of the habitat of the species.

group. It is felt that these data provide concrete evidence in support of the projected swarming groups.

A line has also been drawn connecting the largest oocytes found in each collection before the first swarm in February. The oldest animals in each of these collections ought to be those destined to participate in the first swarm and should therefore represent a single swarming group. This line was used to estimate roughly the growth rate of the oocytes during each phase and to localize the size range during which the growth rate increases. The line suggests an oocyte growth rate of about 1.8μ /day during the second, rapid phase. Oocyte growth rates were also determined for 14 animals with oocytes over 100μ in diameter maintained in the laboratory, as mentioned above. These indicated a growth rate of $1.74 \pm 0.49\mu$ /day. This growth rate estimate is also supported by data from a single unfed animal which was brought into the laboratory with 111μ oocytes. It swarmed 62 days later. Assuming a final oocyte diameter of 200μ , the oocytes in this individual must have grown at a rate of about 1.4μ /day. The average growth rate, during the final period of rapid growth, is thus between 1.6 and 1.7μ /day. The growth rate may not be constant throughout the period of rapid growth in *N. grubei*, and a definite slowing down of growth as the maximum size is approached has been reported for *N. diversicolor* (Clark and Ruston, 1963).

The first swarming takes place in February, and evidence has been found for a swarm each month until June. Each swarm seems to involve fewer animals than the one preceding it, so that the bulk of the population swarms in February and March. In February virtually all the maturing animals in the *Egregia* holdfast habitat disappear; subsequent swarms arise from the *Gastroclonium*. This fact accounts for the lack of data for the spring of 1965. Collections were made during this period, but only from the holdfasts, which were almost totally devoid of maturing animals. After the discovery of *N. grubei* beneath *Gastroclonium*, both habitats were monitored during the spring of 1966. Again mature animals disappeared suddenly and almost completely from the *Egregia* holdfasts during February. However, a significant population remained beneath the *Gastroclonium*

from which at least a few animals swarmed monthly until June.

One of the swarms (represented in Figure 1 by the heavy dotted line over May 1966) has been inferred from the fact that two animals taken from the field on April 26 swarmed simultaneously in the laboratory on May 19. A search of the *Gastroclonium* on May 22 failed to reveal any metamorphosing animals; this is what would be expected if the animals in the laboratory had swarmed simultaneously with a group in the field.

The dates of the full moon for several months of breeding activity during the winter of 1965–1966 have been indicated by vertical dotted bands in Figure 1, since nereid breeding activity has often been correlated with the phase of the moon (Korringa, 1947; Hauenschild, 1966). It should be recalled that the observation of metamorphosing animals in the field must antedate the swarming of these same animals, so that the swarming dates indicated in Figure 1 are all somewhat early. Furthermore, the theory of Hauenschild (1966) suggests that the moon phase might correlate at the point where the oocyte growth rate increases rather than at the time of actual swarming. It is not known whether a latent period occurs between the supposed lunar stimulus and the observed response; the figures presented, do not, in my opinion, either affirm or deny a possible phase-setting relationship with the lunar cycle. The fact that subgroups are separable within the population in early December suggests that some determination of the spawning groups has occurred before the time that the oocyte growth rate has increased within any group. This adds a third point in time for the possible intervention of environmental stimuli in determining the breeding periodicity (see discussion by Clark, 1965).

COMPARISON WITH A SOUTHERN CALIFORNIAN POPULATION

At the outset of this work a definite breeding season had not been expected, since Reish (1954b) reported that the population at Point Fermin showed continual reproduction throughout the year, and that specimens in some stage of metamorphosis could be taken at any time.

The two populations thus differ in the very presence of a breeding season in the population at Pescadero Point.

Constant breeding can be considered as an extremely prolonged breeding season. The average ocean temperature at Point Fermin is several degrees higher than at Pescadero Point, and a lengthening of the breeding season in the southern portion of the range of temperate zone invertebrates is known in other groups, e.g., the sea urchin *Arbacia punctulata* (Harvey, 1956). Additional examples are discussed by Giese (1959) and Clark (1965).

Other differences have been noted between the two populations. The heaviest female reported by Reish weighed approximately 50 mg, and smaller specimens seemed to be the rule, at least in his laboratory-raised animals. The largest female found at Pescadero Point weighed more than 1 gram, and mature females usually weighed in excess of 500 mg; the animals in the Pescadero Point population are thus an order of magnitude heavier than those in the Point Fermin population.

A further difference between the populations involves the site of origin of the oocytes. Reish (1954*b*) found them to originate from a solid tissue within the parapodia, from which clumps of oocytes are released upon achieving a diameter of up to 20 μ . Such a parapodial tissue has never been observed in *N. grubei* from Monterey County, although oogonial proliferation has been demonstrated autoradiographically in small clumps of oogonia floating free in the coelom (Schroeder, 1966). Mature oocytes from animals in the Point Fermin population were found to range in diameter from 162 μ to 380 μ . At Pescadero the size range was much narrower, 190 μ to 210 μ . Oocytes within a given mature female are very uniform in size.

Reish (1954*b*) raised specimens from the Point Fermin population to maturity in his laboratory and found that while they usually metamorphosed after 28 to 29 weeks, exceptional specimens metamorphosed at as early as 14 weeks of age. This variability recalls that observed by Hauenschild (1966) in *Platynereis dumerilii*. Although the life span of a worm from the Pescadero Point population is not known, it must be close to a year at a minimum, and is more likely to be 2 years. The period of

oogenesis alone lasts 7 to 8 months, and much smaller animals than those in which gametes are found may be collected simultaneously. The development time at Pescadero Point is therefore 2 to 4 times as long as the laboratory development time for specimens from the Point Fermin population.

Whether these differences are simply expressions of latitudinal variation within a species, or whether they indicate that a deeper distinction exists between these two populations cannot be determined from the available information. The morphological identity of the two forms has been graciously confirmed by Dr. Reish, who has clarified the taxonomic position of the species in conjunction with his work on its life history (Reish, 1954*a*).

SUMMARY

1. The major algal associates of *Nereis grubei* at Pescadero Point, Monterey County, California, are *Egorgia menziesii* and *Gastroclonium coulteri*. The *Egorgia* holdfasts contain more animals during the fall and winter.
2. At Pescadero Point, *Nereis grubei* breeds from February to June in approximately monthly swarms.
3. Animals collected in December may be assigned to a specific swarming group by determining each animal's average oocyte diameter.
4. The average rate of oocyte growth between 100 μ and 200 μ is 1.6–1.7 μ /day. This represents more rapid growth than is shown by smaller oocytes.
5. The central Californian population differs from that in southern California in its limited breeding season, in the average size of the component individuals, and in the internal site of oogenesis.

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